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The Naturally Occurring Accommodative Response of the Oscar, *Astronotus ocellatus*, to Visual Stimuli

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Observation of the naturally-occurring accommodative response of a highly visual teleost species provides the opportunity to study its stimulus–response accuracy. A video recording system, linked to a computer digitizing program, was used to measure accommodative changes in lens position in the oscar, *Astronotus ocellatus*, in response to known food stimuli. The largest lens deviations occurred along an axis *c.* 22 deg from the pupillary plane. Consistent underaccommodation was reported for the closest of targets, a finding reminiscent of accommodative lag reported in human studies. Copyright © 1996 Elsevier Science Ltd.

Accommodation Teleost Stimulus Response

INTRODUCTION

The fish eye provides a unique opportunity to study accommodation since the lens is easily visible within the eye. Visual species, such as the oscar (*Astronotus ocellatus*), a cichlid, require good accommodative ability for prey identification and capture. The oscar is also easy to maintain and readily available making it a good species in which to study accommodation.

In teleosts, the lens is not deformed during accommodation, as in humans, but is moved within the eye by a smooth muscle, the retractor lentis, that originates at the iris and inserts via a transparent ligament into the lens capsule (Walls, 1942). In its contracted state, the retractor lentis muscle pulls the lens temporally toward the posterior retina. As the muscle relaxes, it allows the lens to move both laterally and nasally away from the retina and toward the cornea. In the human context, the term "accommodated" is used when the ciliary muscle contracts, releasing zonular tension and making the lens more spherical. This increases the refractive power of the lens and brings about a change in the focus of the eye from a far to a near target (Adler-Grinberg, 1986; Hart, 1992). In contrast, the retractor lentis muscle of the oscar is contracted when the eye is focused for a distant target. For consistency, the term "accommodated" will refer to the near focus of the eye and not the condition of tonus of the retractor lentis muscle.

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The accommodative apparatus of teleosts has been the subject of investigation at least since the discovery of the retractor lentis muscle by Wallace in 1834 (Wallace, 1834). Investigators have examined the morphology (Somiya & Tamura, 1973; Andison & Sivak, 1994) and ultrastructure of the musculature (Somiya, 1987), its innervation (Meader, 1936a, 1936b) and the pharmacology of the accommodative system (Tamura, 1957; Meyer & Schwassmann, 1970; Sivak, 1973). However, very little attention has been devoted to studying the dynamic process of accommodation in teleosts. Most of the information regarding the accommodative system in teleosts has been gained under artificial conditions. Lens movements indicative of changes in accommodation have been determined primarily in non-living fish or from excised eyes (Beer, 1894; Tamura, 1957; Kimura & Tamura, 1966; Somiya & Tamura, 1973; Fernald & Wright, 1985a; Somiya, 1987). Following the application of drugs to induce accommodative lens movements, refractive error changes have been monitored using a modified optometer (Tamura, 1957) or a retinoscope (Sivak, 1974). Baylor and Shaw (1962) measured the refractive state of fish in which accommodation was not controlled, but these authors were primarily concerned with determining refractive error and not accommodation. Fernald and Wright (1985b) determined, both directly and computationally, the amplitude of accommodation as a function of fish size in the African cichlid, *Haplochromis burtoni*. These authors used such techniques as electrical stimulation of excised eyes and the injection of parasympatholytic and parasympathomimetic drugs in anaesthetized fish to determine the

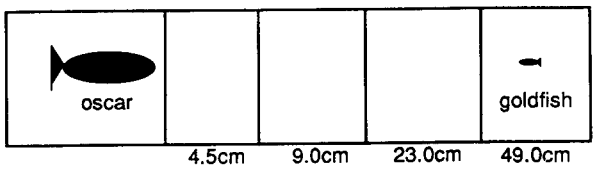

FIGURE 1. Test tank apparatus illustrating average target distances.

accommodative excursion of the lens and associated refractive error changes. The only study of naturally occurring, dynamic accommodative responses in teleosts was by Sivak and Howland (1973). In a preliminary study, these investigators used a video recording system to monitor the accommodative response of rock bass (*Ambloplites rupestris rupestris*) to a feeding stimulus. Both the magnitude and speed of the accommodative response of the rock bass to near and far targets were measured.

Questions regarding the stimulus to accommodation and the accuracy of the animal's response cannot be answered without studying the accommodative response in an alert, cooperative animal. The present study uses a video recording system to observe the naturally occurring accommodative response of the oscar (*A. ocellatus*), in response to visual stimuli and sets out to compare this with the expected accommodative response determined from the stimulus. The refractive state of the fish eye is a matter of uncertainty and controversy (Sivak, 1974). This is because of such factors as axis uncertainty, species differences and uncertainty concerning the effects of chromatic and spherical aberration. The photographic approach used in this study minimizes the need to specify refractive state.

METHODS

The oscars (*A. ocellatus*) used for this study were purchased from a local pet store and maintained in the laboratory in large, aerated tanks. The fish originated from breeding farms in Florida. All experimental procedures were in accordance with the animal utilization guidelines of the University of Waterloo and in accordance with the *Guide to the Care and Use of Experimental Animals* (Canadian Council on Animal Care, 1980). The oscars ranged from 12.0 to 15.5 cm standard length (Hubbs & Lagler, 1967). Feeder goldfish, purchased from a local pet store, were used as a food source and therefore represented a visually meaningful accommodative stimulus for the oscars.

Using a specially designed test tank, the oscars were presented with goldfish at average distances of 4.5, 9.0, 23.0 and 49.0 cm. The order of presentation was randomized to minimize learning or adaptation effects. The tank was constructed of 6 mm clear plexiglass and measured $80 \times 12 \times 11$ cm (Fig. 1). Sliding plexiglass plates were used to position the goldfish and to keep the oscar at the correct distance. White styrofoam barricades were set up around the walls of the test tank to prevent the oscar from being distracted by movements of the experimenter or other objects in the room during testing. The goldfish were, on average, 2.5 cm standard length. A target of this size subtends a visual angle of 29.1 deg at 4.5 cm, 15.5 deg at 9.0 cm, 6.2 deg at 23.0 cm and 2.9 deg at 49.0 cm. These values, however, can only be considered approximate due to possible movements of the target fish and or test fish in addition, neither the oscars nor goldfish stimuli were identical in size.

Accommodative lens movements were recorded using a Hitachi CCD camera mounted on a tripod above the test tank. The camera was linked to a Sony Hi-8 video recorder. The images were simultaneously displayed on a video monitor which enabled the experimenter to monitor the eye and lens movements of the oscar.

An experiment consisted of recording the accommodative lens movements of the oscar in response to the target at each of the four distances. A ruler was held in water at the side of the test tank and focused at the eye level of the oscar to calibrate the images. For each experiment, a pre-measure of the lens position with no target visible (empty field condition) was recorded. A target was introduced at one of the distances and was left in position until the oscar had looked at it at least three times. The target was then removed from the test tank. Before the target was introduced at a different distance, a measure of the position of the lens in the empty field was recorded. Following removal of the target from the fourth test distance, an empty field post-measure of lens position was recorded. This situation was chosen since, in the empty field condition, the eyes of the oscar were diverged, the retractor lentis muscle appeared contracted and the fish was in a state of predator awareness (Sivak & Howland, 1973). In addition, the fact that the measurements of naturally occurring accommodation reported here (see Results) were greater than those induced pharmacologically in the oscar, suggest that these results represent a true description of the range of accommodation (Sivak & Bobier, 1978). Upon completion of an experiment, the oscar was returned to its home tank and fed. A total of ten experiments were run on each of the four oscars.

The video images were analysed using a custom software package which allowed the experimenter to measure discrete distances on the image. Video images including the pupil were chosen for measurement to provide the maximum amount of information regarding the position of the lens. In order to monitor changes in the orientation of the eye, the width of the pupil at its widest point was measured in a line perpendicular to the pupillary plane. Due to the complex nature of the lens movements, seven parameters were chosen to measure the difference between the relaxed and contracted states of the retractor lentis muscle. These parameters included:

1. The posterior inner cornea to lens distance;
2. Posterior pupil edge to lens distance;
3. Anterior pupil edge to lens distance;
4. Anterior inner cornea to lens distance;
5. Inner cornea to lens distance at 45 deg;

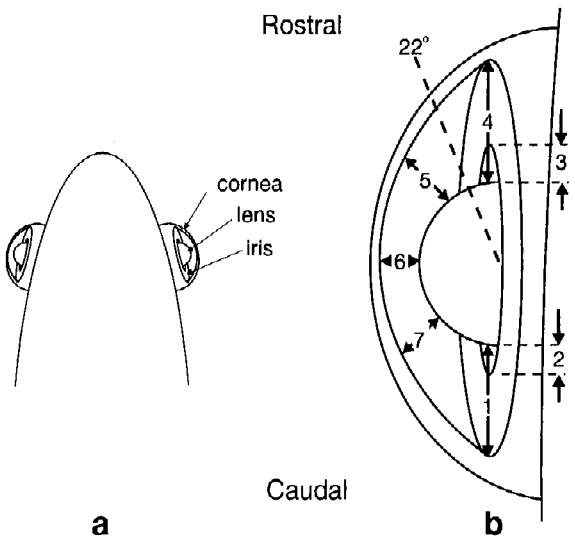

FIGURE 2. (a) Schematic view illustrating eye placement on the oscar. (b) Schematic dorsal view of the left oscar eye. Numbers correspond to the parameters described in the text. Details of the accommodative apparatus may be found in Andison and Sivak (1994).

6. Inner cornea to lens distance at 90 deg; and
7. Inner cornea to lens distance at 135 deg.

With reference to Fig. 2 the measurements made along the seven parameters were relatively insensitive to tilts of the eye, on the order of ± 15 deg, since the axis of rotation of the eye was observed to correspond approximately with the centre of curvature of the cornea. Measurement error was limited by the pixel size on the television screen and was calculated to equal ± 0.03 mm.

The effect of the accommodative lens movement, in dioptres, was determined with respect to the focal length of the lens and compared with the expected values of the stimuli.

Lens equivalent focal lengths of two fish, O3 and O4, were determined using freshly excised lenses placed in an automated laser scanner (Sivak *et al.*, 1987, 1989). The average lens equivalent focal lengths of fishes O3 and O4 were 6.19 ± 0.05 mm and 5.17 ± 0.10 mm, respectively. Since lens diameter has been demonstrated to closely covary with both standard length and body weight in a cichlid fish (Fernald & Wright, 1985b), the focal length values of O1 and O2 (5.68 mm) were interpolated using the body length data of O3 and O4.

The power of a lens in water of focal length 5.68 mm is 234.15 D, calculated using the formula $F = \frac{n'}{f'}$, where n' is the refractive index of water (1.33) and f' is the focal length of the lens expressed in metres. The refractive power of the eye changes as the lens moves during accommodation. If the total measured difference in lens position between the relaxed and contracted states of the retractor lentis muscle is 0.50 mm, adding and subtracting half of this value to the focal length in the above formula will give the range of the power change in dioptres (224.28–244.94 D), and thus the change in accommodation (20.66 D) (Sivak, 1972). This approach is consistent with the effort to avoid contaminating the issue of accommodation with the uncertainty of refractive state. A positive change in accommodation is expected for parameters 1, 2 and 7 and a negative change is expected for parameters 3, 4, 5 and 6 since the lens moves in a rostro-lateral direction during relaxation of the retractor lentis muscle.

The stimulus to accommodation, F, was calculated using the formula, $F = \frac{n'}{l}$, where n' is the refractive index of water (1.33) and l is each of the four target distances expressed in metres.

TABLE 1. Summary of the difference (± SEM), in millimeters, in lens position of relaxed minus contracted muscle states of the four oscars for parameters 1–7 and 22 deg for the four target distances

Parameter	O1	O2	O3	O4
1				
(49.0 cm)	0.11 ± 0.03	0.08 ± 0.02	0.14 ± 0.04	0.08 ± 0.01
(23.0 cm)	0.13 ± 0.02	0.10 ± 0.03	0.14 ± 0.03	0.18 ± 0.03
(9.0 cm)	0.32 ± 0.03	0.13 ± 0.03	0.45 ± 0.05	0.26 ± 0.03
(4.5 cm)	0.54 ± 0.04	0.18 ± 0.06	0.55 ± 0.04	0.40 ± 0.05
2				
(49.0 cm)	0.09 ± 0.04	0.05 ± 0.01	0.06 ± 0.01	0.15 ± 0.00
(23.0 cm)	0.10 ± 0.03	0.04 ± 0.01	0.11 ± 0.02	0.21 ± 0.06
(9.0 cm)	0.29 ± 0.03	0.09 ± 0.02	0.33 ± 0.04	0.25 ± 0.05
(4.5 cm)	0.46 ± 0.04	0.22 ± 0.06	0.45 ± 0.02	0.32 ± 0.05
3				
(49.0 cm)	−0.10 ± 0.05	0.04 ± 0.01	0.06 ± 0.03	0.07 ± 0.03
(23.0 cm)	−0.12 ± 0.04	−0.04 ± 0.01	−0.11 ± 0.02	−0.12 ± 0.04
(9.0 cm)	−0.32 ± 0.06	−0.15 ± 0.02	−0.44 ± 0.05	−0.24 ± 0.05
(4.5 cm)	−0.54 ± 0.05	−0.37 ± 0.07	−0.50 ± 0.04	−0.31 ± 0.03
4				
(49.0 cm)	0.13 ± 0.03	0.08 ± 0.02	−0.06 ± 0.01	0.20 ± 0.04
(23.0 cm)	0.13 ± 0.02	0.08 ± 0.02	−0.15 ± 0.04	0.11 ± 0.03
(9.0 cm)	−0.29 ± 0.04	−0.12 ± 0.02	−0.40 ± 0.05	−0.15 ± 0.03
(4.5 cm)	−0.48 ± 0.05	−0.23 ± 0.04	−0.52 ± 0.05	−0.24 ± 0.04
5				
(49.0 cm)	−0.19 ± 0.08	−0.11 ± 0.01	−0.13 ± 0.02	−0.09 ± 0.02
(23.0 cm)	−0.22 ± 0.07	−0.10 ± 0.02	−0.11 ± 0.02	−0.10 ± 0.02
(9.0 cm)	−0.38 ± 0.08	−0.12 ± 0.02	−0.39 ± 0.04	−0.17 ± 0.03
(4.5 cm)	−0.56 ± 0.07	−0.28 ± 0.02	−0.44 ± 0.03	−0.26 ± 0.04
6				
(49.0 cm)	−0.11 ± 0.04	−0.07 ± 0.01	−0.07 ± 0.02	−0.04 ± 0.01
(23.0 cm)	−0.08 ± 0.02	−0.08 ± 0.01	−0.08 ± 0.02	−0.07 ± 0.01
(9.0 cm)	−0.21 ± 0.02	−0.08 ± 0.02	−0.22 ± 0.02	−0.11 ± 0.01
(4.5 cm)	−0.26 ± 0.03	−0.22 ± 0.02	−0.21 ± 0.02	−0.12 ± 0.02
7				
(49.0 cm)	0.08 ± 0.02	−0.07 ± 0.02	0.06 ± 0.02	−0.04 ± 0.01
(23.0 cm)	0.06 ± 0.02	0.26 ± 0.21	0.05 ± 0.01	0.05 ± 0.01
(9.0 cm)	0.10 ± 0.03	−0.06 ± 0.02	0.10 ± 0.02	0.08 ± 0.02
(4.5 cm)	0.15 ± 0.03	0.34 ± 0.24	0.19 ± 0.03	0.09 ± 0.03
22 deg				
(49.0 cm)	−0.14 ± 0.03	−0.12 ± 0.02	−0.15 ± 0.01	−0.10 ± 0.02
(23.0 cm)	−0.19 ± 0.04	−0.12 ± 0.02	−0.19 ± 0.02	−0.12 ± 0.03
(9.0 cm)	−0.35 ± 0.06	−0.14 ± 0.03	−0.49 ± 0.05	−0.27 ± 0.03
(4.5 cm)	−0.54 ± 0.07	−0.34 ± 0.05	−0.62 ± 0.06	−0.33 ± 0.05

RESULTS

A total of 645 video images were selected and measured for analysis. These images represented the best examples of lens position in the contracted and relaxed states of the retractor lentis muscle and clearly showed the relationship between the lens and cornea.

TABLE 2. Summary of the calculated differences (± SEM) between the relaxed and contracted muscle states, in dioptres, of the four oscars along parameters 1, 2, 3, 5 and 22 deg for each target distance

Parameter	O1	O2	O3	O4	Average (*A*)	Stimulus (*S*)	Difference (*S*−*A*)	*t* (α = 0.05)
1								
(49.0 cm)	4.40 ± 0.60	3.21 ± 0.89	4.75 ± 1.34	3.77 ± 0.68	4.03 ± 0.34	3.17	0.86	2.52
(23.0 cm)	5.30 ± 0.93	3.92 ± 1.06	4.90 ± 1.01	8.79 ± 1.50	5.72 ± 1.06	5.78	0.06	–0.05
(9.0 cm)	13.18 ± 0.87	5.38 ± 1.14	15.61 ± 1.60	13.12 ± 1.24	11.82 ± 2.22	14.78	2.96	–1.33
(4.5 cm)	22.49 ± 1.41	7.37 ± 2.44	19.15 ± 1.25	19.97 ± 2.34	17.25 ± 3.37	29.56	12.31	–3.65*
2								
(49.0 cm)	3.81 ± 1.52	1.97 ± 0.35	1.96 ± 0.31	7.60 ± 0.00	3.83 ± 1.33	3.17	0.66	0.50
(23.0 cm)	4.03 ± 1.49	1.84 ± 0.47	3.87 ± 0.63	10.37 ± 3.01	5.03 ± 1.85	5.78	0.75	–0.41
(9.0 cm)	11.84 ± 1.12	3.89 ± 0.86	11.61 ± 1.34	12.33 ± 2.64	9.92 ± 2.02	14.78	4.86	–2.41
(4.5 cm)	19.17 ± 1.40	9.16 ± 2.28	15.52 ± 0.72	16.02 ± 2.44	14.97 ± 2.10	29.56	14.59	–6.96*
3								
(49.0 cm)	4.18 ± 1.41	1.70 ± 0.53	2.21 ± 1.00	3.38 ± 1.44	2.87 ± 0.56	3.17	0.30	–0.54
(23.0 cm)	4.92 ± 1.21	1.67 ± 0.45	3.70 ± 0.76	6.00 ± 1.92	4.07 ± 0.93	5.78	1.71	–1.84
(9.0 cm)	13.19 ± 1.65	6.24 ± 1.01	15.35 ± 1.68	12.03 ± 2.32	11.70 ± 1.95	14.78	3.07	–1.58
(4.5 cm)	22.49 ± 1.83	15.42 ± 2.71	17.33 ± 1.35	18.08 ± 2.89	18.33 ± 1.49	29.56	11.23	–7.51*
5								
(49.0 cm)	7.97 ± 1.64	4.50 ± 0.57	4.43 ± 0.82	4.58 ± 0.75	5.37 ± 0.87	3.17	2.20	2.54
(23.0 cm)	8.98 ± 1.51	4.07 ± 0.80	3.71 ± 0.73	5.10 ± 1.18	5.47 ± 1.21	5.78	0.31	–0.26
(9.0 cm)	15.79 ± 1.90	4.95 ± 0.90	13.55 ± 1.39	8.49 ± 1.50	10.69 ± 2.45	14.78	4.09	–1.67
(4.5 cm)	23.19 ± 2.08	11.51 ± 0.77	15.32 ± 1.13	12.86 ± 1.86	15.72 ± 2.61	29.56	13.84	–5.30*
22 deg								
(49.0 cm)	5.93 ± 1.31	4.87 ± 0.87	5.26 ± 0.47	4.90 ± 1.21	5.24 ± 0.25	3.17	2.07	8.44*
(23.0 cm)	7.69 ± 1.60	4.92 ± 0.75	6.74 ± 0.78	5.90 ± 1.34	6.31 ± 0.59	5.78	0.53	–0.90
(9.0 cm)	14.59 ± 2.34	5.70 ± 1.26	17.10 ± 1.65	13.27 ± 1.70	12.66 ± 2.45	14.78	2.12	–0.86
(4.5 cm)	22.37 ± 2.79	13.96 ± 2.16	21.42 ± 2.22	16.40 ± 2.37	18.54 ± 2.01	29.56	11.02	–5.48*

*Significant difference.

Table 1 provides a summary of the difference in lens position of relaxed minus contracted states of the retractor lentis muscle for each of the four target distances along each of the seven parameters in millimeters. Negative signs reflect a decrease in distance between the lens and cornea during relaxation of the retractor lentis muscle as the oscars fixated the targets.

A *t*-test was used to determine whether a significant difference exists between the accommodative stimulus and the average experimental accommodative response for each parameter (1–7) (Dowdy & Wearden, 1983). The absolute differences between the target vergences and response values were used in the *t*-test calculations since it was the relative change in position of the lens that was of interest. The values marked with an asterisk in Table 2 indicate a significant difference exists between the experimental and expected results (d.f. = 3, $P = 0.05$).

Four parameters (1, 2, 3 and 5), shown in Table 2, had average differences that were only significantly different from the stimulus at the closest distance (4.5 cm). When the sum of the average differences between the stimulus and the response for each distance was compared for each of these four parameters, the parameters having the least total difference were 1 (16.19 D), 3 (16.23 D) and 5 (20.44 D). These three parameters (1, 3 and 5) were therefore chosen to most closely correspond to the stimuli. Table 2 also provides the average differences between the stimulus and the response at each of the four distances for these parameters. It is interesting to note that for each of the parameters, the greatest difference was at the closest distance (4.5 cm), with the measured responses consistently falling short of the target vergences.

The values measured along distance 2 closely resemble the values of distances 1, 3 and 5. The values measured along 2 are positive, indicating that the lens is moving in the same direction as along distance 1. The values along distance 3 are negative, indicating that the lens is moving in the opposite direction as along distance 1. One would expect the values of 2 and 3 to resemble those of 1, since they all lie along the pupillary plane. The interesting point to note is that the values of 5 (also negative, like 3) are closer to those of 1 and 3 than the values measured along either 6 (90 deg) or 7 (135 deg). Since 1, 3 and 5 most closely matched the target vergences, it appears that the lens must move along a meridian positioned between them (*c.* 22 deg from the pupillary plane).

To confirm the assumption that the greatest displacement occurs along 22 deg, measurements of the inner cornea to lens distance were made at 22 deg from the pupillary plane. These data, labelled "22 deg", appear in Table 1. Clearly, this direction represents the direction of maximum lens movement. Variability in the responses of the oscars along this meridian is apparent. At the closest target distance (4.5 cm), the average response is still about 11 D less than that predicted by the stimulus. Interestingly, there was also a significant difference

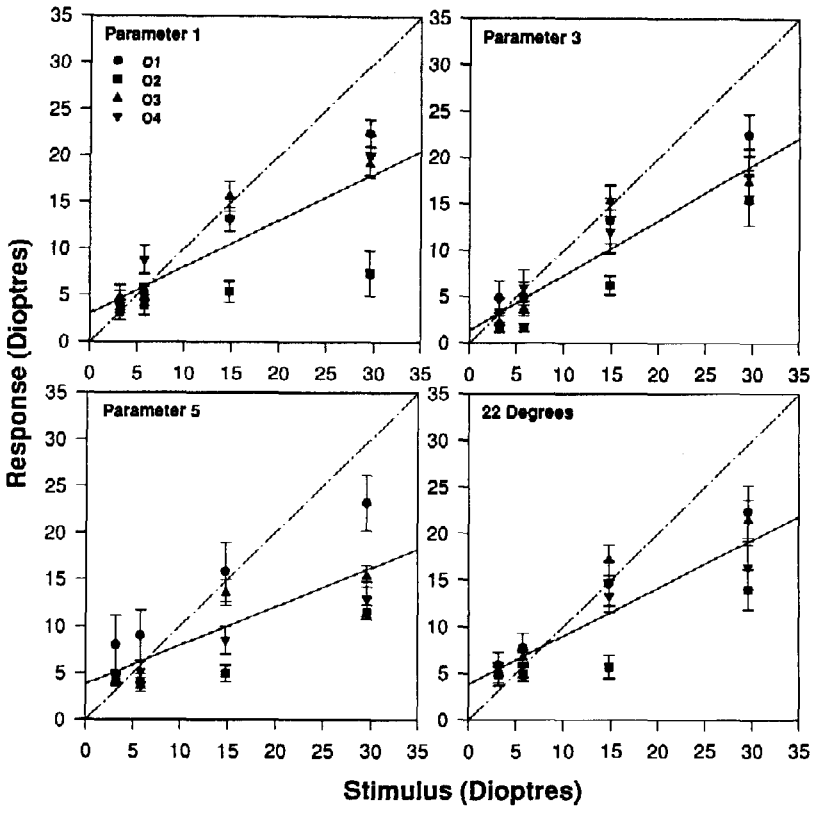

FIGURE 3. Stimulus vs response averages and regression lines plotted for parameters 1, 3, 5 and 22 deg. Dashed line represents the ideal accommodative response (slope = 1). Error bars represent standard error of the mean.

between the response at 22 deg and the furthest target distance.

The poorest match of the stimulus appears to be distance 7, which is positioned along a meridian almost perpendicular to this primary direction of movement. If one examines the data presented in Table 1, the difference between the relaxed and contracted states of the retractor lentis muscle is smaller, on average, than those reported for the other parameters. Thus one would expect the accommodative changes along distance 7 to be very small. The direction in which the largest lens deviation occurs corresponds to the visual axis.

A comparison of the stimulus and response values was made to determine how well the response values matched the stimuli. Figure 3 illustrates the regression analysis performed. Error bars represent the standard error of the mean. Parameter 1 response values vs target vergences were fitted by a regression line ($Y = 0.50X + 3.03$, d.f. = 14, $F = 27.03$, $P < 0.0001$). These values were positively correlated ($R = 0.66$). Parameter 3 response values vs target vergences were fitted by a regression line ($Y = 0.59X + 1.36$, d.f. = 14, $F = 71.76$, $P < 0.0001$). These values were positively correlated ($R = 0.84$). Parameter 5 response values vs target vergences were fitted by a regression line ($Y = 0.41X + 3.83$, d.f. = 14, $F = 21.73$, $P < 0.0001$). These values were positively correlated ($R = 0.61$). The response values along 22 deg vs target vergences were fitted by a regression line ($Y = 0.51X + 3.85$, d.f. = 14, $F = 46.96$, $P < 0.0001$). These values were positively correlated ($R = 0.77$). The regression lines of these parameters have very similar slopes and the response averages were well correlated with the regression lines.

The dashed line in Fig. 3 represents the accommodative stimulus presented to the oscars at each of the four distances. The responses correspond with the stimuli for the two intermediate distances. However, there is a consistent lag of accommodation among the oscars for the largest stimulus (4.5 cm) and a small, but consistent, lead of accommodation for the smallest stimulus (49.0 cm). Note that one of the oscars, O2, showed responses that were substantially smaller, in most cases, than the other three and this has contributed to the variability in the data.

An interesting feature of the data presented in Fig. 3 is that there appears to be some consistency in the error term at each of the four distances. This is most apparent for parameter 5 and provides some indication that the measurement error using this technique is consistent. On average, therefore, the greatest amount of variability appears in the responses made to targets located at the furthest distance.

DISCUSSION

The oscar is a highly visual teleost species that actively pursues its prey (Arora & Sperry, 1963). The oscar must

therefore be capable of maintaining good retinal image quality over a range of distances.

The technique outlined in the present study provides a simple and effective means of measuring the accommodative response in an alert and unrestrained teleost. In this investigation, the extent to which the lens moved with respect to a visual stimulus was measured in five primary directions (0 deg nasal, 45 deg, 90 deg, 135 deg and 180 deg temporal). The direction along which the greatest lens deviation occurred was a combination of the vectors at 0 and 45 deg, or *c.* 22 deg from the pupillary plane. This axis, therefore, corresponds with the visual axis and one would expect to find the greatest density of photoreceptors in the region of the retina along which it extends. Previous investigators have utilized a variety of techniques to determine the direction and range of accommodation in several teleost species. Tamura (1957) measured refractive changes along a number of axes with a refractometer in teleosts under varying artificial conditions. The density of photoreceptors was determined in several areas of the retina and the region having the greatest density corresponded with the axis along which the largest change in refractive error was found. Tamura (1957) called this axis the visual axis, stating that it was the line of most acute vision. Tamura and Wisby (1963) compared photographs of the relative positions of the lens, induced in a variety of living and non-living pelagic fishes, with the receptor density counts from a number of retinal regions in order to determine the visual axis and range of accommodation. Both of these studies determined that the visual axis corresponds with the largest lens deviation and the area of the retina having the greatest density of photoreceptors. It has been reported that a strong relationship exists among the primary axis of accommodation, retinal regions having the greatest receptor densities and feeding behavior (Tamura, 1957; Tamura & Wisby, 1963; Fernald & Wright, 1985b).

The pupil of the oscar eye is oval in shape, the long axis corresponding to the nasotemporal direction. This configuration is an indication that accommodative lens movements occur primarily along this axis (Sivak, 1978). Tamura (1957) related the axis of accommodation to the point of attachment of the suspensory ligament to the lens and with the orientation of the retractor lentis muscle. In a previous study, Andison and Sivak (1994) reported observations of two motions of the lens during accommodation; one in the nasotemporal direction and one in the mediolateral direction. The nasotemporal movement was observed to be larger. These observations were supported by light and scanning electron microscopy which indicated that there are two muscle fibre orientations within the body of the single retractor lentis muscle of the oscar (Andison & Sivak, 1994). The results of the present study also support the earlier observations. The average accommodative lens movement along 90 deg (parameter 6) was consistently smaller, and significantly different from the stimulus, than the movement observed along either 45 deg (parameter 5) or along the pupillary axis (parameter 1). Refer to Table 1.

The difference between the accommodative stimulus and the accommodative response represents the lead or lag of accommodation (Daum, 1991). Only a portion of the typical human accommodative stimulus–response curve shows correspondence between the response and the stimulus. The response curve lies above the stimulus line for the furthest stimuli and below for the nearest stimuli. These non-corresponding portions demonstrate accommodative lead (in the form of hyperopia) and lag (in the form of myopia), respectively. In humans, accommodative lag changes as a function of fixation distance so that as fixation distance decreases, accommodative lag increases (Daum, 1991).

Investigators have long been aware that accommodation may not match that expected based on target distance (Toates, 1972). The error which exists is necessary if accommodation is explained on the basis of a feedback–control system which proposes that accommodation acts as a proportional controller. In this system, defocus is the error detected by the retina which guides the ciliary muscle to minimize the defocus. However, since accommodation is a proportional controller, the error cannot eliminate itself completely, otherwise no feedback (error) would be available to maintain the tonus of the ciliary muscle (Toates, 1972). The defocus information is needed by the autonomic nervous system to guide the ciliary muscle to produce the correct accommodative response. Thus, accommodative lead and lag are functionally significant in the proportional feedback system. When the eye changes its focus or is in a steady state, overaccommodation (lead) and underaccommodation (lag) act as the stimuli for sympathetic and parasympathetic innervation, respectively. Thus accommodative lead will stimulate sympathetic discharge and inhibit parasympathetic discharge and accommodative lag will stimulate parasympathetic discharge and inhibit sympathetic discharge (Toates, 1972).

In the present study, the responses of all fish demonstrated a lag of accommodation for the closest targets, and accommodative lead for the furthest target. A significant difference between the stimulus and furthest target was only reported along 22 deg, indicating that the greatest accommodative lead occurs along this axis. Accommodative lead and lag were evident for each of the parameters (1, 3, 5 and 22 deg) illustrated in Fig. 3. On average, the greatest variability existed in the responses to the furthest targets. This may be an indication that these targets were falling within the depth of focus of the eye, suggesting that a certain amount of focusing error is tolerated by this system without detriment to the quality of the image (Bennett & Rabbetts, 1989).

The results of this experiment correspond well with the findings of human accommodation studies. This in itself is interesting given the morphological and physiological differences between the human and teleost accommodative systems. Perhaps this is evidence that the control of accommodation at higher centres is quite similar among

vertebrates, despite the various visual adaptations necessary for each species to function in its ecological niche.

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